SOUND PRODUCTION AND ASSOCIATED MORPHOLOGY IN MALE JUMPING SPIDERS OF THE *HABRONATTUS AGILIS* SPECIES GROUP (ARANEAE, SALTICIDAE)

Wayne P. Maddison

Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138 USA

and

Gail E. Stratton[1]

Department of Biology
Bradley University
Peoria, Illinois 61625 USA

ABSTRACT

Stridulating male jumping spiders in the *Habronattus agilis* species group have a file on the back of the cephalothorax and stout, curved setae on the front of the abdomen. Compared to non-stridulating *Habronattus* speces, stridulators have modified sclerites around the pedicel, and much more massive muscles running from the lorum to the dorsal carapace apodeme and from the side of the pedicel to the epigastric plate. Sound mostly below 3500 Hz is produced during courtship when the abdomen is vibrated up and down against the back of the carapace. When most of the scraper setae are ablated, the sound is diminished. Stridulation may have evolved from the common salticid behavior of abdomen twitching.

INTRODUCTION

The well-sighted jumping spiders often appear to communicate primarily by vision, with striking ornaments and complex courtship motions, yet recently stridulation with probable communicatory function has been reported in three genera. Male *Phidippus mystaceus* (Hentz) have a plectrum on the palpal tibia which rubs against a file on the cymbium during courtship (Edwards 1981). In *Saitis michaelseni* Simon, males scrape stout setae on the front of the abdomen against a file on the back of the carapace (Gwynne and Dadour 1985). A very similar mechanism had been earlier described in *Habronattus agilis* (Banks) and its relatives by Maddison (1982, reported as *Pellenes agilis*), on whose preliminary report we here elaborate.

Habronattus agilis and other species in the *agilis* species group (see Griswold 1987:181) live in sandy habitats in North America, usually on grass tufts, other vegetation, and dry leaves. Males have distinctive vertical fringes on the first legs

[1]Present address: Department of Biology, Albion College, Albion, Michigan 49224 USA.

which are exposed during courtship (Fig. 1). The following species in the group were studied by us: *H. agilis* (Banks), *H. alachua* Griswold, *H. cognatus* (Peckham and Peckham), *H. conjunctus* (Banks), *H. elegans* (Peckham and Peckham), *H. georgiensis* Chamberlin and Ivie, and *H. peckhami* (Banks). Five additional species in different species groups were also studied: *H. borealis* (Banks), *H. americanus* (Keyserling), *H. oregonensis* (Peckham and Peckham), *H. calcaratus* (Banks), and *H. decorus* (Blackwall).

MATERIAL AND METHODS

Collecting localities.—*H. cognatus* specimens were collected on Long Point, Lake Erie, Ontario (SEM's, sclerites, musculature), Bruce Beach, Lake Huron, Ontario (sclerites), Warren Dunes State Park, Michigan (behavior recordings and experiments). The other *agilis*-group specimens were: *H. agilis*, from Crane's Beach, Essex Co., Massachusetts (behavior); *H. conjunctus*, from Grays Well Road, east of El Centro, Imperial Co., California (behavior recordings); *H. elegans*, from Chilao Campground, Los Angeles Co., Quail Lake, Los Angeles Co., and Camarillo, Ventura Co., all from California (behavior recordings); *H. alachua*, from Ocala National Forest, Marion Co., Florida (behavior, SEM); *H. peckhami*, from Stinson Beach, Marin Co., California (behavior). *H. borealis* specimens were from the Hamilton Beach Strip, Hamilton, Ontario (SEMs, sclerites, musculature), Long Point, Ontario (musculature), and Warren Dunes State Park (behavior). *H. americanus* were from Nevada City, Madison Co., Montana (sclerites), Austin, Nevada and Beaver Creek, Gunnison Co., Colorado (musculature) and South Fork Campground, San Bernardino Mts., California (behavior), *H. calcaratus maddisoni* Griswold from Rigaud, Quebec (musculature, sclerites), *H. decorus* from Pulaski Park, Delta Co., Michigan (sclerites) and Gull Lake, Alberta (musculature), and *H. oregonensis* from Furry Creek, British Columbia (musculature) and the Nacimiento-Fergusson Road, Monterey Co., California (behavior). Specimens were identified by the senior author with the aid of information, unpublished at the time, from Charles Griswold (see Griswold 1987).

Morphology.—Males to be examined with a scanning electron microscope (SEM) were first critical-point-dried. To observe sclerites, internal tissues were digested in pepsin for a few days and fully cleared overnight in cold 1 N KOH. To understand musculature, numerous dissections were made of specimens of *H. borealis* and *H. cognatus* fixed in Kahle's solution, along with a few dissections of alcohol-fixed *H. borealis, cognatus, calcaratus, americanus, oregonensis,* and *decorus.* Figures 6 and 8 were done with a camera lucida on an Olympus BH2® brightfield compound microscope from paraffin-dipped specimens sectioned by hand with a razor blade and mounted in Euparal, supplemented with information from the dissections and other sections. Figures 7 and 9 were done of muscles in alcohol with the same camera lucida and microscope with incident fiber-optics light.

Behavior and sound.—Courtship behaviors were videotaped for 4 males of *H. cognatus*, 3 of *H. elegans*, 3 of *H. conjunctus*, 2 of *H. oregonensis*, and one male each of *H. borealis* and *H. americanus*. All videotaping was done in a sound-treated 23-24° C room courtesy of the Speech and Hearing Department of Bradley
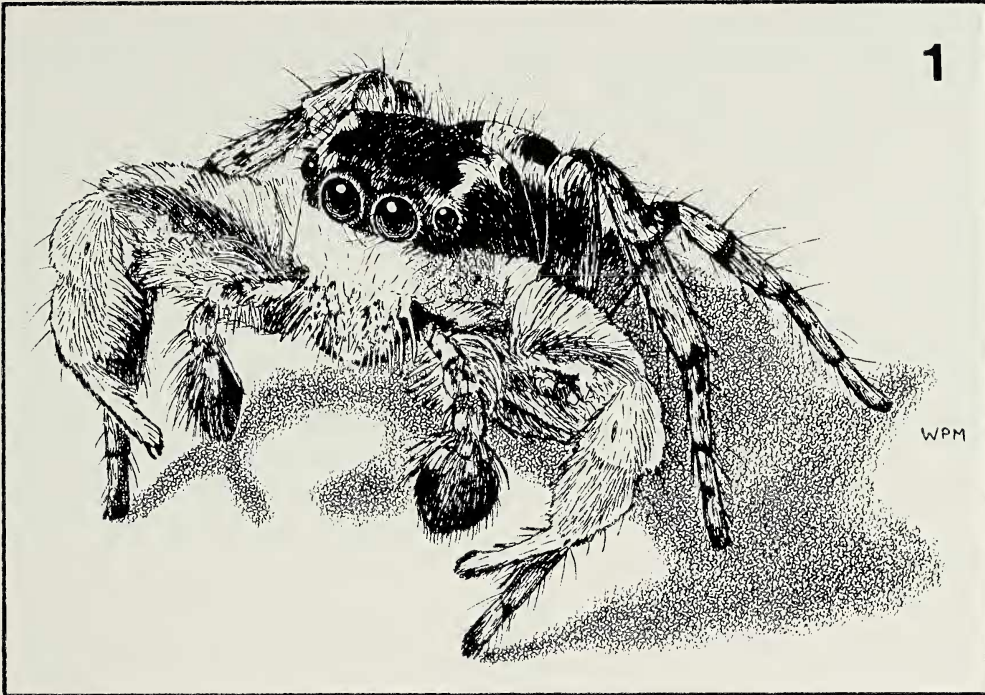
Fig. 1.—Male *Habronattus cognatus* in courtship pose (from Uetz and Stratton 1983; used by permission of Pergamon Press).

University. Video recordings were made with a JVC color video camera (Model 6X-N74 with 105 mm macro lens) connected to a Pentax Video Recorder (Model PV-R1000A). Sound recordings were made of spiders placed on a light piece of cardboard (22 X 16.5 cm) taped over a Pressure Zone Microphone® ("Sound Grabber"™, Crown International, Inc.), connected to the videorecorder. The cardboard acted as a sounding board, as might dry leaves in the spider's natural habitat. We did not attempt to isolate a substrate-borne component of the sound. The videotapes were used to determine durations and frequencies of some of the prominent behaviors. Sounds recorded on the videotapes were rerecorded on cassette tape and analyzed using a Kay Elemetrics Sonagraph® model 6061B.

Ablation experiments.—Ablation operations were performed to investigate the importance of the prominent setae on the front of the abdomen. In two males (#1 and #2) of *H. cognatus* the two largest "scraper" setae above the pedicel were scraped off with a microscalpel while the spider was CO_2-anesthetized in an operation lasting about five minutes. One other male (#3) was anesthetized and sham operated. After about three hours, recordings were made from all males. Later the same day, a second operation was performed in the same manner on the two previously-operated males, to remove some of the smaller "scraper" setae beside the pedicel on the front of the abdomen. We were unable to remove all of these setae. Later examination of the males after preservation showed that in male #1, six setae remained on the left side, none on the right; in male #2, three setae remained on the left, none on the right, and there were at least five empty sockets; on both males the large setae had been cleanly removed by the first ablation. Male #3 was once again sham operated. Later examination showed it
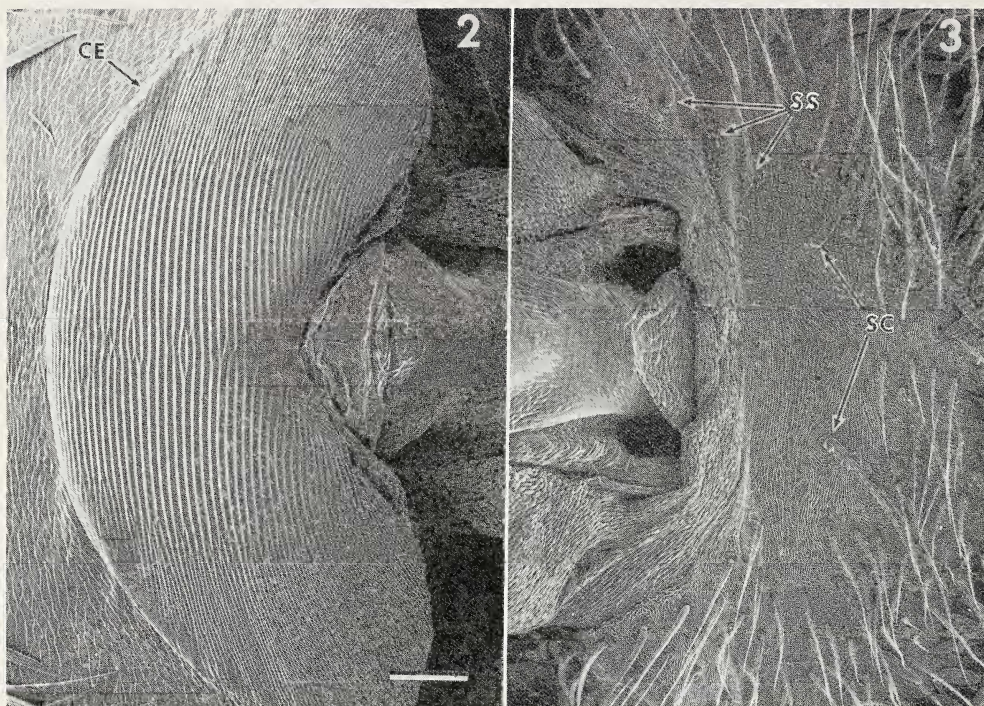
Figs. 2, 3.—*Habronattus cognatus* male: 2, posterior of cephalothorax showing stridulatory file (CE = lower edge of carapace); 3, anterior of abdomen showing two large scraper setae (SC) and several smaller scraper setae (SS). Scale line = 0.1 mm.

had 9 small and 2 large scraper setae. Two hours elapsed between the second operation and the recording. The spiders showed no ill effects from the operations. Sounds were recorded and analyzed as described above.

MORPHOLOGY

Stridulatory apparatus.—An abdomen-carapace stridulatory mechanism, consisting of a file on the back of the cephalothorax and scraper setae on the front of the abdomen, is present in males of all species examined of the *agilis* group (*H. agilis, H. alachua, H. cognatus, H. conjunctus, H. elegans, H. georgiensis, H. peckhami*). Similar mechanisms are known from hahniids, theridiids, gnaphosids and clubionids (Legendre 1963; Uetz and Stratton 1982), and the salticid *Saitis michaelseni* (Gwynne and Dadour 1985).

The file on the cephalothorax consists of parallel ridges (Fig. 2). The spacing of ridges seems approximately constant from one species to the next, but only two species were measured (from SEMs). The central part of the file has the widest ridge spacing, about 10-11 μm in one male of *H. alachua*. Laterally, the ridges branch and the spacing becomes much narrower, about 4-4.5 μm in *H. cognatus* and 4 μm in *H. alachua*. Females, and males of other groups, lack the file. The file is not part of the carapace proper, but is instead a wide sclerotized portion of the arthrodial membrane just beneath the back of the carapace, as indicated by the carapace-edge ridge lying just above it (Figs. 2, 4 CE) and the attachment of muscle 75 (Fig. 6). The file of *Saitis michaelseni* is apparently also below the
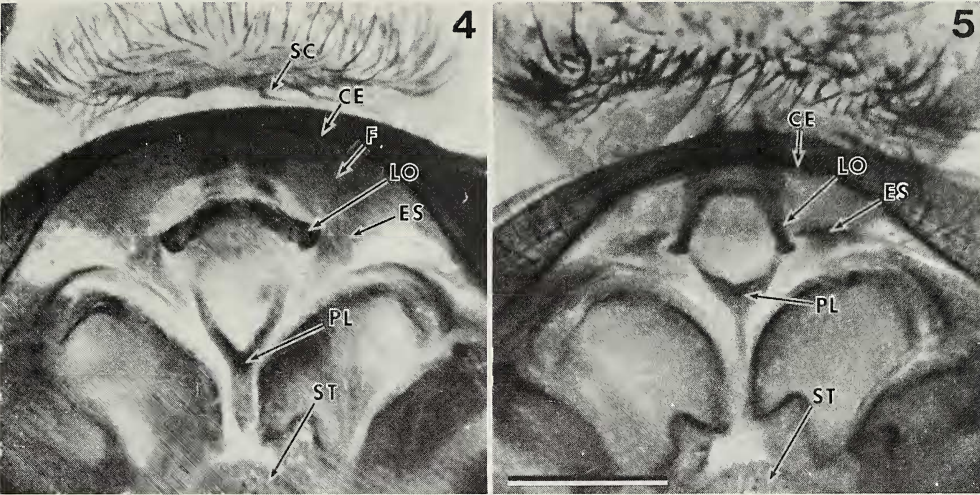
Figs. 4, 5.—Sclerites near pedicel, oblique view from anterior dorsal of cleared integument with most of carapace cut away (CE = carapace edge; F = file viewed from inside; LO = lorum; PL = plagula; SC = scraper seta; ST = sternum); 4, *Habronattus cognatus* male (stridulator; note robust plagula and divergent arms of lorum); 5, *Habronattus calcaratus* male (non-stridulator). Scale line approximately 0.5 mm.

carapace, given Gwynne and Dadour's (1985) SEMs and the captions to their figures b and c on plate I.

The front of the abdomen bears two large curved setae just above the pedicel (Fig. 3 SC) and a series of 4-7 smaller curved setae on each side of the pedicel in males of the *agilis* group (Fig. 3 SS). Both the larger and smaller setae arise and then bend to parallel the surface. The large setae presumably would contact the central coarse part of the file and the smaller setae would contact the lateral fine part of the file. Females of the group have setae similar to, but smaller than, those of males. Males and females of other species groups have no such curved setae.

Sclerites.—Males of the one *agilis*-group species studied, *H. cognatus*, have a number of unusual features of the sclerites near the pedicel. The lorum has anterior arms more robust and divergent than in non-*agilis*-group species studied, *H. calcaratus, H. borealis, H. americanus,* and *H. decorus* (Figs. 4 and 5, LO). The plagula is much more robust than in *H. borealis* or *H. calcaratus* (Figs. 4 and 5, PL), but only slightly more robust than in *H. decorus* or *H. americanus.* The surface of the abdomen bearing the scraper setae and the epigastric plate are both more heavily sclerotized in males of the *agilis* group than in males of the other *Habronattus* species studied (except *H. americanus*, whose abdominal front is also fairly heavily sclerotized). The sternum of *agilis*-group males is unusually convex (Fig. 6), possibly to accommodate the brain crowded downward by the large lorum-apodeme muscles (see below).

Muscles.—Figures 6-9 show the pedicel musculature of *H. cognatus* (Figs. 6, 7) and *H. borealis* (Figs. 8, 9). Each muscle is labeled with the number of the presumably-homologous muscle in *Latrodectus* (Whitehead and Rempel 1959). Because some muscles differ from those previously reported for spiders, we discuss them briefly here. Whitehead and Rempel report two lorum-carapace muscles in *Latrodectus*, #73 (unpaired) and #75 (paired), while Palmgren (1978)
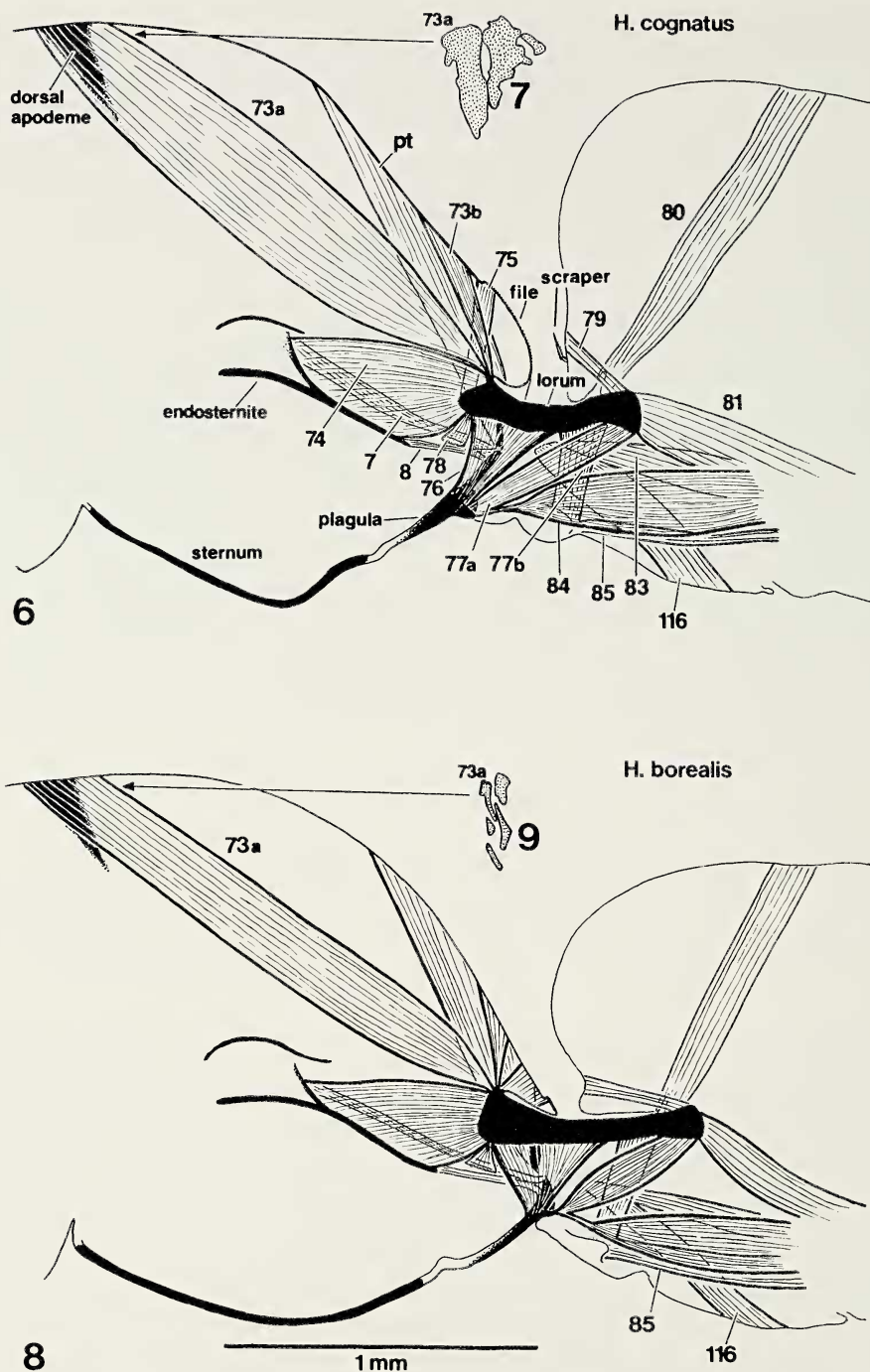
Figs. 6-9.—Sagittal sections showing musculature of the pedicel region (6, 8), with insets (7, 9) showing exposed carapace attachment surface of dissected muscle 73a: 6, 7, *Habronattus cognatus*; 8, 9, *H. borealis*. Muscle numbering follows Whitehead and Rempel (1959), with exceptions noted in text.

figured only a single lorum-carapace muscle in salticids, his "lt" which he considered homologous to #73 of *Latrodectus*. We found three lorum-carapace muscles, which we call #73a (paired, medially on lorum to dorsal apodeme), #73b (unclear whether paired or unpaired, medially on lorum to back of carapace) and #75 (paired, laterally on lorum to back of carapace). Palmgren's figures suggest that his "lt" is our #73b. Palmgren apparently overlooked #73a, which we have seen in all salticids we have dissected (except *Lyssomanes*), including members of the genera *Acragus, Cocalodes, Habrocestum, Menemerus, Phidippus, Portia, Salticus, Sitticus,* and *Talavera.* We have also seen it in an oxyopid (*Oxyopes* sp.). In some of these (*Acragus, Cocalodes, Menemerus, Portia,* and *Oxyopes*) the muscle attaches directly to the dorsal apodeme, while in the others (including *Habronattus*) most or all of the fibers attach to the carapace on either side of the apodeme. Palmgren also did not describe our #75, and he suggested that Whitehead and Rempel's #75 is homologous to his plagulo-tergalis muscle (pt), which it is not. Whitehead and Rempel failed to describe Palmgren's "pt," possibly because they felt that "pt" was just part of the carapace compressor #31, which it may be, for it arises not from the plagula proper but from a small (epimeral?) sclerite closely associated with the lateral arm of the plagula (Figs. 4, 5, ES). Other workers have described only two dorsoventral pedicel compressors (see Brown 1939) whereas we found three, muscles 76, 77a, and 77b. What we label as #77b is a thin sheet and may have been overlooked. Muscles 83, 85 and 116 do not attach to the plagula but to the lateral, ventral and lateral membranous walls, respectively, of the pedicel.

Three musculature differences between *H. cognatus* and *H. borealis* males were notable. The lorum-dorsal apodeme muscle (73a) is not only thicker vertically in *H. cognatus* (Figs. 6, 8), but is much thicker laterally, so that the area of carapace attachment is more than threefold greater (Figs. 7, 9). This difference in thickness was consistent in all specimens examined (nine or more of each species), and is not due just to greater size of *H. cognatus,* for in fact *H. borealis* males are slightly longer and probably more massive. Four other non-*agilis*-group species were also dissected for muscle 73a, and in each the muscle was only about as massive as in *H. borealis,* having a small area of carapace attachment (*H. calcaratus* 1 male, *H. americanus* 2 males, *H. oregonensis* 1 male, *H. decorus* 1 male). The ventral pedicel-abdominal endosternite muscle (85) is thinner in *H. cognatus* than in *H. borealis,* though this does not show well in the illustrations. The lateral pedicel-epigastric plate muscle (116) is considerably broader in *H. cognatus.*

The much greater development of muscles #73a and 116 in *H. cognatus* may be related to the fact that it is a stridulator whereas *H. borealis* and the other four species examined are not (with the possible exception of *H. americanus*; see below). Both *H. cognatus* and *H. borealis* make noise with abdominal motions (see below), but the motion is gentle in *H. borealis,* while in *H. cognatus* the abdomen is vibrated vigorously up and down against the cephalothorax. Muscles #73a and 116 are parallel to the direction of abdominal motion during stridulation, and may supply much of the power for pulling the abdomen up against the carapace. Still, any conclusions about the functional significance of these musculature differences must be viewed as tentative, for the system is partly hydraulic and the effect of a given muscle contraction is difficult to predict.

BEHAVIOR AND SOUND

Courtship behavior of male *Habronattus cognatus*.—In the initial stages of courtship three discrete behaviors may be recognized, in each of which some sound is produced. Stationary Abdomen Vibration (SAV) occurs when the male is standing still. The abdomen is raised, such that the ventral surface is parallel to the ground, and is vibrated up and down, striking the back of the cephalothorax in a series of discrete pulses (number of pulses/second = mean 5.5 ± 0.6 SD, range 4.5-6.8, n = 8 bouts of SAV by male #1; duration of each pulse 0.12-0.15 second). Sonagram analyses of the sound produced were made for three males. The most prominent sound component is composed of frequencies from about 1 kHz to 3.5 kHz (Figs. 10, 13; the male of Figs. 16, 17 showed a different pattern). There is also a component along the baseline of the sonagram, below 500 Hz. Occasionally a weaker component at 5-6 kHz appears on the sonagrams (Fig. 13). Our recordings showed no component of sound between 8 kHz and 16 kHz (above the range shown in the figures). Between each pulse the sonagrams show a series of vertical lines of 1-3.5 kHz, each line possibly the result of a single stroke of the abdomen (Figs. 10, 13). The sounds produced during SAV are much fainter than those of *Saitis michaelseni*, which are audible from 3-5 m (Gwynne and Dadour 1985). The mean duration of a bout of SAV was 6.0 seconds ($\pm$ 4.3 SD, range 1.8-14.5, n = 8 bouts by male #1).

Abdomen Bobbing (AB) also occurs while the male is standing still, and alternates with SAV. The abdomen is lowered (but not so as to touch the ground), and twitched slightly down and up every 0.3-0.6 seconds, each twitch producing a sound pulse below 500 Hz (Fig. 16). The series of sound pulses resembles the purring of a cat. The mean duration of a bout of AB was 5.4 seconds ($\pm$ 3.4 SD, range 1.1-12.4, n = 8 bouts by male #1).

The Leg Curl display (LC) includes pulsed abdomen vibration like SAV but has in addition vigorous leg and body movements. Typically the male will hold the first pair of legs to the side with the femur either horizontal or slightly above horizontal and the more distal segments curled downward and inward (Fig. 1). With the legs so held, the male sidles quickly and flicks the first pair of legs and palps outward, apparently in synchrony with the pulses of abdomen vibration. The pulses of abdomen vibration occur at higher frequency than during SAV (about 8 pulses/second). The sound produced during LC was much like that produced during SAV, but the sonagram was more irregular, probably because of noise made by the first legs. The mean duration of a bout of LC was 2.4 seconds ($\pm$ 1.7 SD, range 1.0-8.9, n = 8 bouts by male #1). LC is often preceded by SAV, and immediately after LC the male may return to SAV and AB with the legs remaining in the curled position. Though the LC display resembles the hunched-leg agonistic display used by various salticids (e.g., Jackson 1978, 1986a, 1986b), the LC display we observed is no doubt a courtship display given the consistent use of LC by males toward females (seen in all of the approximately 100 bouts of male to female display observed in five species of the *agilis* group), the vigor of its motions, and the failure of males to open the fangs during it.

The later stages of courtship have been seen only a few times in *H. cognatus*, and videotaped only once. The male approaches with the first pair of legs held outstretched and forward, sometimes flickering them up and down (Leg Flickering, LF). The male reaches and touches the female on her front femur with
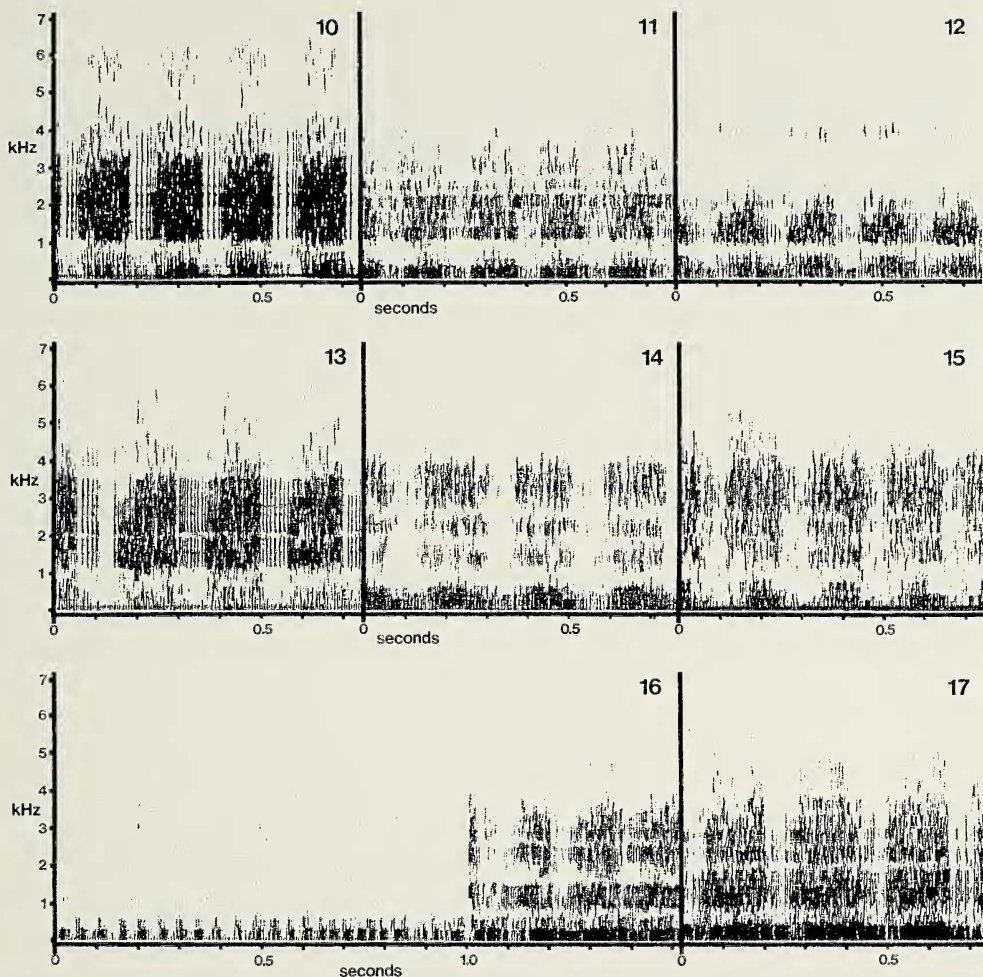
Figs. 10-17.—Sonagrams from *Habronattus cognatus* courtship, all from Stationary Abdomen Vibration (SAV) except the first part of 16, which is from Abdomen Bobbing (AB): 10-12, Male #1, 10 before ablation operations; 11, after first ablation operation; 12, after second ablation operation; 13-15, male #2; 13, before ablation operations; 14, after first ablation operation; 15, after second ablation operation; 16-17, male #3; 16, before sham operation (AB until 1.0 second, SAV after 1.0 second); 17, after sham operation.

his first pair of legs before mounting. Our equipment detected no sounds during these later stages save the footsteps of the male.

Courtship behavior of other *agilis*-group members.—We have observed courtship behavior in five other *agilis*-group species. Two species, *H. conjunctus* and *H. elegans*, were videotaped and their sounds recorded. *H. elegans* (three males) display was much like that of *H. cognatus*, with SAV and AB alternating with LC. The frequency of pulses of abdominal vibration during SAV was 4.8-5.5 pulses/second (*n* = 2 bouts for one male from Chilao Campground). Each pulse of sound had one prominent component below 500 Hz, and another component (prominent though not as in *H. cognatus*) at 1.5 to 3 kHz (Fig. 18). The sonagram is different than those for *H. cognatus*, but given the variation observed in *H. cognatus* (Figs. 10, 16) the difference may not be consistent. *H.*
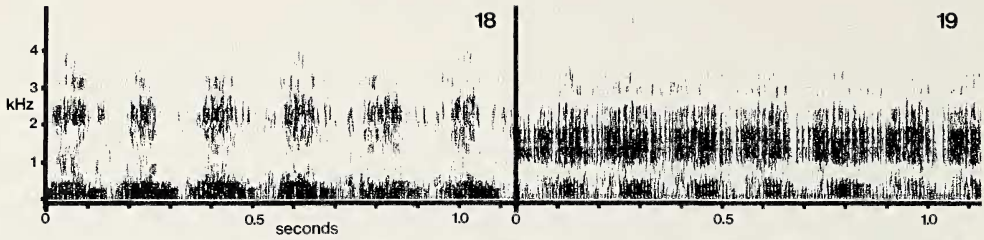
Figs. 18-19.—Sonagrams from Stationary Abdomen Vibration of *Habronattus elegans* (18) and *H. conjunctus* (19) courtship.

conjunctus (three males) likewise had a very similar SAV, AB, and LC. The frequency of pulses of abdominal vibration during SAV was 6.3 pulses/second (*n* = 1 for one male from Imperial Co., California). Each pulse had one prominent component below 500 Hz, and another at 1-2.5 kHz (Fig. 19). However, this species only infrequently performed SAV, AB and LC, instead spending more time in the later LF stage and often reaching and touching the female. In the LF stage the legs were sometimes held apart, sometimes forward, but never curled inward. They were flicked up and down in a jerky fashion as the male proceeded more or less straight toward the female. Just before attempting mounting, the male touched the female's femora, as in *H. cognatus*. No sound was heard during LF or later stages. Richman (1982a) described courtship for this species (under the name *Pellenes arizonensis*). He apparently saw both LC ("courtship...often began with the male positioning his front legs in a wide-spread stance, than [sic] moving in a zigzag, crab-like fashion toward the female") and LF ("the front legs were extended and waved a few times"), and the premount femur touch, but no comment is given on sound or the relative frequency of the early and late stages.

We previously observed three *agilis*-group species, *H. agilis* (one male), *H. alachua* (one male) and *H. peckhami* (one male), without videotaping. In all the leg curl display appeared as in *H. cognatus*, with the first legs curled and flicking while the male sidles and vibrates the abdomen. The pulsed rasping noise produced by the abdomen was heard, but not recorded, in *H. agilis* and *H. peckhami*. Later stages in LF and premount femoral touching were also observed once in *H. agilis*. Emerton (1909: 230) describes and figures what is apparently LF in *H. agilis*. Richman (1982b) gives a brief description of the display of another agilis-group species, *H. georgiensis* (under the name *Pellenes agilis*), indicating that the abdomen is twitched up and down.

These observations indicate much uniformity of courtship, at least to a human's eyes and ears, throughout the species group. Except for the greater frequency of LF in *H. conjunctus*, we detected no significant differences in courtship of these species, all showing LC, and those studied closely showing SAV and AB. If these taxa are indeed all reproductively isolated, females may discriminate by color patterns on the face and first legs, which differ markedly among the species.

Courtship behavior of other *Habronattus*.—For purposes of comparison, the courtship of three *Habronattus* species in different species groups were also videotaped: *H. borealis, H. americanus* and *H. oregonensis*. In none of these species is there an obvious file and scraper mechanism on the carapace and abdomen, and yet in two of these species abdominal movements produces an easily recorded sound.

In *H. borealis* courtship the first legs are raised and held forward as the male sidles and waves his palps over his front femora. The male then moves the palps forward and stops walking, flicks the first legs' tips a few times, then alternately shuffles the left and right third legs, then waves the first legs inwards a few times, then waves the first legs rapidly as he proceeds to mount. In the second last stage, each time the legs are waved inward the abdomen is depressed and a faint buzz can be heard. The abdomen does not contact the substrate, nor does it rub against the carapace.

In *H. americanus* the male sidles with first legs bowed and held forward and the palps down and apart. When close he suddenly stands high, reaches forward and rapidly pulls the first legs down and in against the substratum and/or the back of the female's first pair of legs, as he simultaneously lowers the front of his abdomen down against the back of his carapace. Relatively loud sounds are produced by this, possibly with contributions from both the first legs and the abdomen. While *H. americanus* males have an unmodified carapace and lack scraper setae, the front of the abdomen is heavily sclerotized and rugose, and stridulation may be occurring.

In *H. oregonensis* the male holds the first legs to the side (see figure on p. 359 of Peckham and Peckham 1909) and waves them slightly as he sidles. When close to the female he holds the first legs forward and vibrates one or the other. Our recordings showed no sounds nor were abdominal vibrations seen.

ABLATION EXPERIMENTS

Thus far we have described a scraper and file, and the abdominal movements and sounds produced, but the question remains: are the sounds heard during courtship of the *agilis* group due solely to the rubbing of the scraper setae against the file? Our ablation experiments indicate that the scraper setae do indeed contribute sound, but that these may not be the only sources of sound. The results are preliminary, for we performed incomplete ablation experiments on only two males. Also, the substrate-borne component of the sound, which we did not directly measure, may be important to the spider.

After the first ablation of the large scraper setae, the sound produced by abdominal vibration during SAV was diminished and changed in quality, both to our ears and according to the sonagrams. The prominent 1-3.5 kHz component was lessened in both males #1 and #2, but the component below 500 Hz seemed unaffected (Figs. 11, 14). Frequencies of 2.5-3.5 kHz were especially diminished in male #1, whereas in male #2 the 1-2.5 kHz sounds were diminished. Because of the different responses of the two males, the exact frequencies contributed by the scraper setae is uncertain. The vertical lines between pulses were no longer clear on the sonagrams after ablation, suggesting that they may be made by the large scraper setae; however, these lines also seemed absent from the recordings of male #3 whose setae were intact. The second ablation produced little change from the first (Figs. 12, 15), although the sounds appeared to have diminished further. The drop in absolute sound intensities is not accurately known, because recorded intensity depended on the spider's exact position on the cardboard. Still, to our ears the sound after both operations seemed to be at least half as loud as the pre-operation sound. Neither ablation affected (to our ears) the purring sound from

AB, as expected since the abdomen does not contact the cephalothorax during AB. Male #3's sound was essentially unchanged following its sham operation (Fig. 17).

Given that ablation of 1/2 to 3/4 of the setae decreased the sound but not proportionately, it appears that sound below 500 Hz and perhaps some between 1 and 3.5 kHz is produced without the aid of these setae. How then is it produced? The common salticid courtship behavior of twitching the abdomen down and up (Jackson 1982) actually produces a low frequency sound (at or below 500 Hz), even though the twitch of the abdomen seems slight and there is no carapace or substratum contact (Maddison and Stratton 1988); the sound may be produced by the legs recoiling against the substrate with each abdominal twitch. *Habronattus cognatus* also performs this abdomen twitching behavior: we have called it "AB" and the sound produced "purring". If such subtle motion of the abdomen can make audible sound, then the vigorous abdomen vibration during SAV may produce much of its sound by the same mechanism, and the scraper setae merely add a component, albeit a strong one, by stridulation. This is consistent with the observation that frequencies below 500 Hz were relatively untouched by ablation (Figs. 11, 12, 14, 15).

The communicatory significance of the abdominal vibration during courtship needs to be determined, although it is difficult to use females of these species for behavioral assays, for they rarely accept males in the laboratory. It would also be necessary to determine the relative importance of air- versus substrate-borne vibrations. Further research should examine these parameters.

Another topic for future research is the possible use of stridulation in other contexts by these species, such as during threat display of male-male interactions. We have observed male-male interactions in *Habronattus cognatus* only once; the first legs were held curled as in LC, the carapace was raised and the abdomen bent down toward the substrate. The first legs and palpi were stationary during the display. The depressed position of the abdomen might suggest that stridulation could not be accomplished, but given our limited observations we must allow for the possibility that stridulation might generally be a part of male-male threat display.

Perhaps the abdomen vibration and stridulation in the *agilis* group and in *Saitis michaelseni* have evolved as extreme forms of the abdominal twitching common in salticids (Gwynne and Dadour 1985). If so, then both the *agilis* group and *S. michaelseni* have enhanced the sound from twitching with very similar stridulatory mechanisms. Other salticids may have taken other routes to enhancing the sound. A number of euophryines in both the New World (species placed in *Cobanus, Agobardus, Antillattus, Siloca*) and Old World (*Stagetillus, Eustirognathus*) have the integument just anterior to the tracheal spiracle sclerotized and swollen into a bump (see Bryant 1943, Fig. 91). Behavioral observations need to be made on these genera to test whether the bump might be used percussively against the substrate.

A broader survey of species is clearly needed to reveal the patterns and diversity in the evolution of noisemaking in salticids. While stridulatory mechanisms such as that found in the *Habronattus agilis* group may be rare in salticids, many species make noises (Maddison and Stratton 1988). The importance of acoustic communication to salticids has probably been underestimated.

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